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H. Lu
Texas AgriLife Research

Jackie C. Rudd
Texas AgriLife Research and Extension Center, jcrudd@ag.tamu.edu

J. D. Burd
USDA ARS

Y. Weng
USDA-ARS, yiqun.weng@ars.usda.gov

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Molecular mapping of greenbug resistance genes *Gb2* and *Gb6* in T1AL.1RS wheat-rye translocations

H. Lu[1], J. C. Rudd[1], J. D. Burd[2] and Y. Weng[1,3,4]

[1]Texas AgriLife Research – Amarillo, 6500 Amarillo Blvd West, Amarillo, TX 79106, USA; [2]USDA ARS, 1301 N Western Rd, Stillwater, OK 74074, USA; [3]Present address: USDA-ARS Vegetable Crops Research Unit, Horticulture Department, University of Wisconsin, Madison, WI 53706, USA; [4]Corresponding author, E-mail: yiqun.weng@ars.usda.gov

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Abstract

Two greenbug resistance genes *Gb2* and *Gb6* derived from the same donor rye line 'Insave', are present in wheat germplasm lines 'Amigo' and 'GRS1201', respectively as 1AL.1RS wheat-rye translocations. The allelic relationship between the two genes has not been determined, and no molecular markers for *Gb6* are available. In this study, molecular mapping of *Gb2* and *Gb6* was performed in a mapping population derived from a cross between 'N96L9970' (*Gb6Gb6*) and 'TAM 107' (*Gb2Gb2*). Segregation among $F_{2:3}$ families of host responses to infestation of greenbug biotypes E and KS-1 revealed that *Gb2* and *Gb6* were different linked loci in 1RS. *Gb2* and *Gb6* were 15.8 cM apart with *Gb6* being distal to *Gb2*. Despite the low number of marker polymorphisms between the parental lines, eight markers linked with *Gb2* and *Gb6* were identified. The closest marker, *XIA294*, was 11.4 cM proximal to *Gb2*. Deletion mapping indicated that both *Gb2* and *Gb6* were physically located in the satellite region of 1RS.

Key words: *Triticum aestivum* — *Secale cereale* — wheat-rye translocation — molecular marker — aphid resistance

Greenbug, *Schizaphis graminum* (Rondani), is an economically important aphid pest of small grain crops in many parts of the world, and it is the most important insect pest of wheat (*Triticum aestivum* L.) in the southern Great Plains of the USA (Webster and Kenkel 1995, Kindler et al. 2003). This species has been especially problematic due to periodic changes in biotypes. Over 20 greenbug biotypes have been recognized (Porter et al. 1997, Burd and Porter 2006). In the past 30 years, the prevailing greenbug biotypes have shifted from C to E and E to I in southern Great Plains (Berzonsky et al. 2002). At present, the greenbug resistance gene *Gb3* deployed in wheat cultivars 'TAM 110' (Lazar et al. 1997) and 'TAM 112' (PI 643143) provides effective protection from greenbug damage. However, due to the potential for virulence changes in greenbug populations, use of a single resistance gene for control represents a significant risk. Development and deployment of additional resistance sources is desirable in wheat breeding programmes.

Seven (*Gb1*–*Gb7*) greenbug resistance genes have been identified in wheat relatives and transferred into the wheat genome (Tyler et al. 1987, Porter et al. 1994, Weng et al. 2005). The greenbug resistance gene *Gb1* identified in durum wheat, *T. turgidum* ssp. *durum* Desf., confers resistance to biotype A, which is no longer detected in Great Plains greenbug populations (Porter et al. 1997). *Gb3*, *Gb4* and *Gb7* are derived from *Aegilops tauschii* Coss. and are located on wheat chromosome arm 7DL (Joppa et al. 1980, Martin et al. 1982, Weng and Lazar 2002, Zhu et al. 2004, 2005, Weng et al. 2005). A chromosome segment containing *Gb5* from *Ae. speltoides* L. was transferred into wheat via a translocation involving 7AL (Dubcovsky et al. 1998).

Greenbug resistance genes, *Gb2* and *Gb6*, on chromosome arm 1RS (Hollenhorst and Joppa 1983, Porter et al. 1991), were transferred to wheat from rye (*Secale cereale* L.). *Gb2* and *Gb6* exist as T1AL.1RS translocations in wheat cultivar 'Amigo' (Porter et al. 1987) and germplasm line 'GRS1201' (Porter et al. 1991), respectively. Interestingly, both *Gb2* and *Gb6* were derived from 'Insave' rye (Porter et al. 1991). *Gb2* is ineffective against biotypes C, E and I, whereas *Gb6* confers resistance to a much wider spectrum of greenbug biotypes than *Gb2* or *Gb3* (Burd and Porter 2006). The allelic relationship between *Gb2* and *Gb6* has not been studied in detail, and no molecular markers specific for *Gb6* are available. The objectives of this study were to (1) understand the allelic relationship between *Gb2* and *Gb6*, (2) identify molecular markers for the two resistance genes, and (3) physically map *Gb2* and *Gb6* to sub-chromosome arm regions in 1RS.

Materials and Methods

Plant materials: The mapping population used in this study consisted of 151 $F_{2:3}$ families developed from the cross 'N96L9970' (PI619231) × 'TAM 107' (PI495594). 'TAM 107' is a winter wheat cultivar carrying the dominant greenbug resistance gene *Gb2* originating from 'Amigo' (Porter et al. 1987) and 'N96L9970', a germplasm line developed from the cross 'GRS1201' × 'TAM 202', has *Gb6* from 'GRS1201' (Graybosch et al. 2004).

Common wheat varieties 'Chinese Spring' ('CS') and 'Pavon 76' ('Pavon'), rye variety 'Insave', CS rye chromosome arm 1RS deletion lines 1RS-4 and 1RS-6 (Friebe et al. 2000), and four rye 1R-wheat 1B recombinant lines (Pavon T-1, Pavon T-3, Pavon 1B + 3 and Pavon 1B + 38, Lukaszewski 2000) were used for physical mapping of marker loci in 1RS.

Greenbug resistance assessment: Plants from each F_3 family were tested for responses to infestation of greenbug biotypes E and KS-1. Reactions of F_3 families to greenbug biotype E were evaluated at Texas AgriLife Research, Bushland, Texas, USA as described by Weng and Lazar (2002). Briefly, 15 seeds of each F_3 family, the parents, susceptible control 'TAM 105' and resistant control 'TAM 110' were germinated in 30 cm rows, with 18 rows in 30 × 50 cm plastic flats. About 500 aphids were scattered over each flat to initiate infestation.

Infested plant materials were kept in a growth chamber at 22°C, 14 h daylength. Ten to fourteen days after infestation, 'TAM 110' and resistant seedlings only showed light symptoms similar to senescence in older leaves, whereas 'TAM 105' and susceptible plants were all dead and mostly dried (Weng et al. 2004). Therefore, each plant was scored qualitatively as either resistant or susceptible. The phenotypic data were used to infer F_2 genotypes at the *Gb6* locus.

To determine the genotypes at the *Gb2* locus, a similar infestation test was performed with greenbug biotype KS-1 at the USDA-ARS laboratory, Stillwater, OK, USA.

Molecular marker analysis: Ninety-six molecular markers previously mapped in Triticeae homoeologous group-1 short arms were selected for initial mapping. All markers, including SSRs, STS and RFLPs used in this study, were PCR-based and the primers for each marker were commercially synthesized. The parental lines were screened for polymorphisms with these primers using PCR and agarose gel electrophoresis. Polymorphic markers were then applied in the F_2 mapping population. A framework map was constructed to determine the sub-chromosome arm locations of *Gb2* and *Gb6* in 1RS. Based on initial mapping results, 162 (258 in total) additional markers detecting loci that were genetically or physically mapped in the *Gb2* and *Gb6* regions were tested. Primer information for the three new markers mapped in the present study is listed in Table 1.

Leaf tissue from each F_2 plant was collected and stored at −80°C. Total genomic DNA was extracted as described in Weng et al. (2000). For marker analysis, a 10 µl PCR reaction contained 1.0 µl 10× PCR buffer, 1.0 mM $MgCl_2$, 0.4 mM dNTP mix, 2 pM each of the two primers, 50 ng template DNA, and 0.5 U *Taq* DNA polymerase. Amplifications were performed in an Applied Biosystems (Foster City, CA, USA) 2720 thermocycler with the touchdown programme as described in Weng and Lazar (2002): an initial 3 min denaturation at 95°C; six cycles of 45 s at 94°C, 5 min at 68°C, 1 min at 72°C, with the annealing temperature being reduced by 2°C per cycle; followed by eight cycles of 45 s at 94°C, 2 min at 58°C, 1 min at 72°C, with the annealing temperature being reduced by 1°C per cycle; then 25 cycles of 45 s at 94°C, 2 min at 50°C, 1 min at 72°C; and ending with 5 min at 72°C. The PCR products were resolved in a 3.5% agarose gel in a 1× TBE buffer with ethidium bromide added to the gel.

A sub-set of EST-derived primer pairs was used for single nucleotide polymorphism (SNP) detection between parental lines. When a primer pair of a particular marker amplified a clear, bright, but monomorphic band from both parents, the bands were excised from the agarose gel, purified with the QIAquick Gel Extraction kit (QIAGEN, Valencia, CA, USA), and sequenced by Agencourt (Beverly, MA, USA). The sequences of both parents were compared for SNP discovery.

Deletion mapping: To determine the sub-chromosomal locations of the two resistance genes, *Gb2*-linked molecular markers IA294 and BCD762 were PCR tested for presence or absence in target DNA fragments among a deletion mapping panel including 'CS', 'Pavon', 'Insave', 1RS-4, 1RS-6, Pavon T-1, Pavon T-3, Pavon 1B + 3 and Pavon 1B + 38. These cytogenetic stocks have variable sized 1RS segments in wheat genetic backgrounds, enabling physical mapping of rye- or wheat-specific markers to a sub-arm region in 1RS (Lukaszewski 1997, 2000, Friebe et al. 2000).

Table 1: Primer sequences of EST markers linked to *Gb2* and *Gb6*

Marker	Primer sequence (5′ → 3′)	Note
BE587049	ATATCTCAACCAACTTCACAAAGTC CATTGTTTAAAAAGAGGGGATATG	
BE704796	TATACACCAACAAGTAGCGACAATA AAACAAACCTTCAGTATCTTCTCAC	SNP
BE705057	AAAGTCGTTTCTTAGAGGTGAATCT ATTGTGAGCATTTACTCTGTGTCTT	

Data analysis: Chi-square (χ^2) tests for goodness of fit to theoretical ratios were performed on the $F_{2:3}$ segregation data. A linkage map was constructed with MAPMAKER 3.0 (Lander et al. 1987) using a LOD threshold of 3.0 and the Kosambi mapping function (Kosambi 1944).

Results

Inheritance of greenbug resistance

Frequencies of F_2 genotypes for the *Gb2* and *Gb6* loci established from separate tests on F_3 lines with greenbug biotypes E and KS-1 are given in Table 2. The combined frequencies of genotypes departed significantly ($P < 0.0001$) from independent segregation at two loci. Segregations at the individual loci conformed with 1 : 2 : 1 ratios, although that at the *Gb6* was only marginally acceptable ($P = 0.0685$). The linkage chi-squared value was highly significant ($P < 0.0001$) indicating that *Gb2* and *Gb6* were linked loci in rye 1RS.

Linkage analysis of *Gb2*, *Gb6* with molecular markers

When 'N96L9970' and 'TAM 107' were screened for polymorphism for 96 previously mapped markers that detected loci in Triticeae homoeologous group-1S chromosomes (mainly rye 1RS), variation between them was extremely low: only four (IA294, BMAC0213, BCD762, and BARC148) were polymorphic. Using MAPMAKER, a framework map in the *Gb2*, *Gb6* region ordered the markers loci and two resistance genes as *Gb6-Gb2-XIA294-Xbmac0213-Xbcd762-Xbarc148*. The cumulative map distance between *Gb2* and the marker locus *Xbcd762* was 42.1 cM (Fig. 1), similar to 51 cM on a previously published linkage map for *Gb2* (Mater et al. 2004).

Based on the initial map, an additional set of 162 markers previously used for mapping in Triticeae homoeologous group-1 short arms (mainly 1RS) were assessed for polymorphisms between 'N96L9970' and 'TAM 107'. Three (BE587094, BE705057 and TSM61) polymorphic markers were identified and mapped (Fig. 1). Since the polymorphism level was extremely low using agarose gels, single nucleotide polymorphism (SNP) detection was explored for a subset of non-polymorphic markers. Forty-eight pairs of monomorphic DNA fragments PCR-amplified from both 'N96L9970' and 'TAM 107' were excised from the gels, purified, and sequenced. One SNP marker (BE704796) was identified.

Of the eight loci detected by polymorphic markers, six were mapped in the population at a LOD threshold of 3.0 (Fig. 1). The remaining two, BMAC0213 and BARC148, were placed at their most likely positions on the linkage map (Fig. 1). All marker loci were proximal to *Gb2*, with *XIA294* being the closest and 11.4 cM from *Gb2*. *Gb6* was 15.8 cM distal to *Gb2* (Fig. 1).

Table 2: Frequency of F_2 genotypes at the *Gb2* and *Gb6* loci inferred from F_3 infestations with greenbug biotypes KS-1 and E

	Gb6Gb6	*Gb6gb6*	*gb6gb6*	*Total*
Gb2Gb2	3	10	23	36
Gb2gb2	10	61	3	74
gb2gb2	34	6	1	41
Total	47	77	27	151

Chi-$sq_{1:2:1}$, *Gb2* vs. *gb2*, 2df, 0.39, $P = 0.8228$; Chi-$sq_{1:2:1}$, *Gb6* vs. *gb6*, 2df, 5.36, $P = 0.0685$; Chi-$sq_{linkage}$, 4df, 110, $P = 0.0001$; Chi-$sq_{1:2:1:2:4:2:1:2:1}$, 8df, 141, $P = 0.0001$.

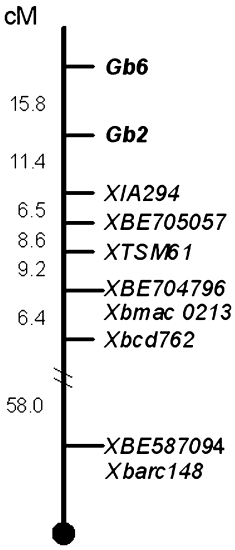

Fig. 1: Genetic map of greenbug resistance genes *Gb2* and *Gb6* in 1RS of wheat-rye chromosome T1AL.1RS translocations. All marker loci were mapped at a LOD threshold of 3.0 except for *Xbmac0213* and *Xbarc148* which were placed at the most likely positions of the linkage map. Numbers to the left are genetic distances in centiMorgans (cM) between adjacent markers or genes. The black circle represents centromere

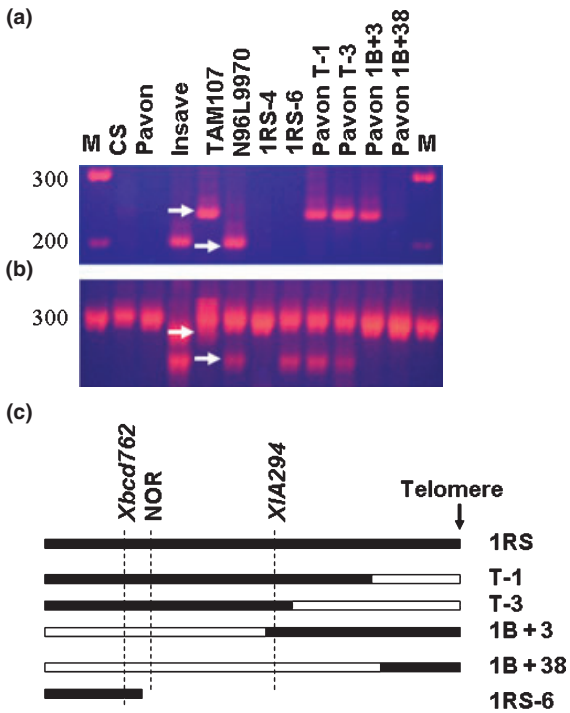

Fig. 2: Physical mapping of molecular markers IA294 and BCD762 in rye chromosome arm 1RS. (a) PCR amplification patterns of primer IA294 in different lines. (b) PCR amplification patterns of primer BCD762. Deletion mapped polymorphic alleles (i.e. markers *XIA294* and *Xbcd762*) are indicated by arrows in (a) and (b). (c) Physical locations of *XIA294* and *Xbcd762* in relation to NOR in 1RS. Rye and wheat chromosome segments are indicated by blackened and empty boxes, respectively. M, size marker. The numbers to the left of the marker lane are fragment sizes (bp)

Physical locations of greenbug resistance loci *Gb2* and *Gb6*

To infer the physical locations of *Gb2* and *Gb6* in chromosome 1RS, two co-dominant markers linked with *Gb2*, IA294 and BCD762 were chosen to characterize a deletion mapping panel consisting of six cytogenetic stocks and relevant parental lines (Fig. 2).

IA294 amplified a single band (Fig. 2a) that was polymorphic between 'TAM 107' (240 bp) and 'N96L9970' (205 bp). No PCR product was amplified in 'CS' and 'Pavon'. The band in 'Insave' was the same as in 'N96L9970'. A single band, which was the same as that in 'TAM 107', was amplified in Pavon T-1, Pavon T-3 and Pavon 1B + 3, but not in Pavon 1B + 38, indicating that the locus *XIA294* was located in the overlapping 1RS regions of Pavon T-1, Pavon T-3 and Pavon 1B + 3 (Fig. 2a and c). No PCR amplification was detected in 1RS-4 and 1RS-6.

Four alleles were detected in the deletion panel with BCD762 (Fig. 2b). The 302 bp fragment present in all lines except 'Insave' is likely to be of common wheat origin. One band (290 bp) was unique to 'Insave' rye. The remaining two bands were polymorphic between 'TAM 107' (298 bp) and 'N96L9970' (270 bp) and were mapped in the population as a co-dominant marker. The 270 bp fragment in 'N96L9970' was the same as in 'Insave' and was present in 1RS-6, Pavon T-1 and Pavon T-3, but absent in 1RS-4, Pavon 1B + 3 and Pavon 1B + 38, suggesting that the *Xbcd762* locus was in the overlapping 1RS regions of Pavon T-1, Pavon T-3 and 1RS-6 (Fig. 2b and c). The deletion line 1RS-6 (Fig. 2c) lacks the satellite part of the short arm, and 1RS-4 (not shown in Fig. 2c) lacks most of the short arm (Friebe et al. 2000). Thus the marker *Xbcd762* locus was proximal to the NOR (nucleolus organizer region) of 1RS, as shown in Fig. 2c.

The physical mapping of these two markers confirmed the chromosome orientation of the linkage map. Both *Gb2* and *Gb6* were located in the satellite region of 1RS with *Gb6* being distal.

Discussion

Although the chi-square analysis supported the 1 : 2 : 1 ratio for segregation at *Gb6* locus, the actual P value of 0.0685 (Table 2) was close to the threshold value (P = 0.05) of significance, a similar phenomenon to that observed by Graybosch et al. (1999). Results from both studies suggested preferential transmission of *Gb6*. However, it was demonstrated that abnormal transmission of genes or markers has little effect on linkage estimates (The and McIntosh 1975, Lorieux et al. 1995).

Gb2 and *Gb6* were shown to be different linked loci in rye chromosome arm 1RS. The 1RS arms in the T1AL.1RS translocations carried by 'TAM 107' and 'N96L9970' are derived from the same rye variety 'Insave'. Graybosch et al. (1999) reported that the two 1RS arms also had different secalin protein components and varying fingerprints of the rye-specific molecular marker PAWS5/S6. It is therefore obvious that 'Insave' is a genetically heterogeneous population (Porter et al. 1991, Sebesta et al. 1995). However, of the 258 molecular markers tested in the study, only eight (3%) were polymorphic between the parents.

Despite of the low degree of polymorphism, we were able to develop a meaningful linkage map for *Gb2* and *Gb6*. *Gb2* was 11.4 cM distal to *XIA294*, and *Gb6* was 15.8 cM distal to *Gb2*. Since *XIA294* was physically mapped in the NOR region, both *Gb2* and *Gb6* should also be distal to NOR in 1RS. This is consistent with Mater et al. (2004), who placed *Gb2* 2.7 cM proximal to the rye seed protein secalin-coding gene *Sec-1*,

which is also located in the NOR region. *Sec-1* was approximately 19 cM proximal to the powdery mildew resistance gene *Pm17* (Mater et al. 2004). The gene *Pm8* in 1RS of the 'Kavkaz' T1BL.1RS translocation was shown to be allelic to *Pm17* (Hsam and Zeller 1997). The map distance between *Gb2* and *Gb6* was 15.8 cM in this study. Therefore, *Gb6* may be near the *Pm* locus.

Chromosome 1RS continues to play an important role in wheat cultivar performance, and wheat-rye translocations are present in the materials of many wheat breeding programmes worldwide (Weng et al. 2007). T1AL.1RS translocations are of particular interest to wheat breeding in the southern Great Plains of the USA for developing wheat cultivars with resistances to multiple insects and pathogens. The T1AL.1RS translocation from 'GRS1201' carries greenbug resistance gene *Gb6* and the 'Amigo'-derived T1AL.1RS confers resistance to the stem rust race Ug99 (Jin and Singh 2006). T1AL.1RS translocations have less deleterious effects on baking quality than the T1BL.1RS translocation (Kumlay et al. 2003). In the present study, eight markers were found to be linked with *Gb2* and *Gb6*, with the closest marker *XIA294* being 11.4 cM from *Gb2*. No marker was identified in the region distal to *Gb2* (Fig. 1). The very low polymorphism between 1RS translocations in 'N96L9970' and 'TAM 107' may hinder future efforts on high resolution mapping of *Gb6* and other genes in this cross. Lukaszewski (1997) developed a series of wheat-rye reconstituted chromosome stocks. One of these stocks has the T1AL.1RS translocation in 'Pavon' background. The 1RS in that stock was from 'Kavkaz', whose 1RS source was rye cultivar 'Petkus' (Schlegel and Korzun 1997). It is well documented that 1RS of the T1BL.1RS translocation in 'Kavkaz' and many derivatives carries multiple disease resistance genes, including leaf rust resistance gene *Lr26*, stripe rust resistance gene *Yr9*, stem rust resistance gene *Sr31*, and powdery mildew resistance gene *Pm8*. Due to the different origins of 1RS in the T1AL.1RS translocations in 'N96L9970' and the 'Pavon' line, there should be more polymorphisms than between the two T1AL.1RS translocations studied in the present work.

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